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**Correlation between Vividness of Visual Imagery and
Echolocation Ability in Sighted, Echo-Naïve People**

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Review

Correlation between Vividness of Visual Imagery and
Echolocation Ability in Sighted, Echo-Naïve People

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Abstract

The ability of humans to echolocate has been recognised since the 1940s. Little is known about what determines individual differences in echolocation ability, however. Although hearing ability has been suggested as an important factor in blind people and sighted trained echolocators, there is evidence to suggest that this may not be the case for sighted novices. Therefore non-auditory aspects of human cognition might be relevant. Previous brain imaging studies have shown activation of the early 'visual', i.e. calcarine, cortex during echolocation in blind echolocation experts, and also during visual imagery in blind and sighted people. Therefore, here we investigated the relationship between echolocation ability and vividness of visual imagery (VVI). 24 sighted echolocation novices completed Marks' (1973) VVI questionnaire and they also performed an echolocation size discrimination task. Furthermore, they participated in a battery of auditory tests that determined their ability to detect fluctuations in sound frequency and intensity, as well as hearing differences between the right and left ear. A correlational analysis revealed a significant relationship between participants' VVI and echolocation ability, i.e. participants with stronger vividness of visual imagery also had higher echolocation ability, even when differences in auditory abilities were taken into account. In terms of underlying mechanisms, we suggest that either the use of visual imagery is a strategy for echolocation, or that visual imagery and echolocation both depend on the ability to recruit calcarine cortex for cognitive tasks that do not rely on retinal input.

Keywords: Visual Cortex, Calcarine, Audition, Hearing, Blindness, Cross-Modal

1. Introduction

Echolocation denotes the use of reflected sound waves to retrieve information about the external environment (Griffin 1944). The ability of blind people to avoid silent objects was first noted by Diderot (1749, as cited in Worchel and Dallenbach 1947) who described the ability of his blind acquaintance to perceive obstacles and judge their distance. It was not until the 1940s, however, that auditory cues were established as necessary and sufficient for object detection in blind participants (Supa et al. 1944; Worchel and Dallenbach 1947) and that this ‘obstacle sense’ exhibited by blind people was recognized as being due to the human ability to echolocate (Griffin 1944). Evidence now shows that both blind and sighted people are able to learn to echolocate (e.g. Ammons et al. 1953; Worchel and Mauney 1951) and that reflected sound waves can provide skilled echolocators with a wealth of useful information about the reflecting object - e.g. position, distance, size, and density (for reviews see for example Schenkman and Nilsson 2010; Stoffregen and Pittenger 1995), as well as motion (Rosenblum et al 2000; Thaler et al 2013a). On a purely physical basis, information about these properties is carried through mono- and binaural variations in echo timing, spectrum (pitch) and intensity (loudness), and people may be able to exploit these variables for echolocation (Cotzin and Dallenbach 1950; Papadopoulos et al 2011; Rosenblum et al 2000; Schenkman and Nilsson 2010; 2011; Stoffregen and Pittenger 1995), though the use of one or the other acoustic variable may also depend on the echolocation task people engage in. Remarkably, some expert echolocators are even able to perform accurate object identification using echolocation (Thaler et al. 2011), but the information underlying this skill is unclear to date. Echolocation may have real-life advantages for blind people (Thaler 2013b).

The ability to echolocate differs between those who are blind and sighted as well as within these groups. There is evidence that blind people are better at echolocation than those who are sighted (see Teng and Whitney 2011, for a summary) and one possible reason for this might be that blind people are generally more sensitive to acoustic reverberations (Dufour et al. 2005; Kolarik et al. 2013). There are also substantial differences in echolocation capacities between blind people, with congenital blind children often needing no training (Ashmead et al. 1989), and people who lose vision earlier in life showing better performance (Teng et al. 2012). In sighted people Teng and Whitney (2011) found that all of their sighted novices improved their echolocation ability with regard to size discrimination across multiple sessions, but also that there was variability across participants. Similarly, in an echolocation task designed to assess spatial precision, participants’ performance ranged from complete inability to performances approaching the level of an experienced blind echolocator (Teng and Whitney 2011). The question arises as to what underlies individual differences in echolocation ability. Addressing this could also provide useful information for use in echolocation training.

Considering that echolocation relies on hearing, an obvious hypothesis is that individual differences in hearing abilities underlie individual differences in echolocation. Previous studies which have investigated this found mixed results. Schenkman and Nilsson (2010) found a relationship between echolocation object detection and the difference in auditory thresholds between the two ears in blind participants. They failed to find this relationship in sighted echolocation novices. They also did not find any relationship between echolocation ability and pure tone thresholds in either group. Participants in Schenkman and Nilsson’s (2010) study echolocated by listening to sound recordings that contained sonar emissions and acoustic reverberations. Carlson-Smith and Wiener (1996) looked at a possible relationship between hearing and echolocation abilities in highly trained sighted echolocators. Like Schenkman and Nilsson (2010) they did not find a relationship between echolocation ability and pure tone thresholds, but did find that those participants who were better at detecting variations in intensity and pitch (relative to a 500 Hz tone) were also better at using echolocation to detect objects and doorways. This relationship could be explained assuming that participants in this study echolocated obstacles by exploiting variations in echo intensity and pitch. Participants in Carlson-Smith and Wiener’s (1996) study echolocated by listening to acoustic

reverberations that arose from their own foot-steps while walking. In sum, the evidence to date suggests that although hearing ability may play a role for echolocation ability in blind people and trained sighted echolocators, this may not be the case for sighted novices. Consequently, here we consider a possible relationship between a non-auditory aspect of human cognition and echolocation ability.

In a recent fMRI study investigating the neural correlates of echolocation in people, it was found that the calcarine cortex (CC), i.e. early 'visual' cortex, of blind echolocation experts was more active during the processing of echo sounds as compared to the processing of echo-less control sounds (Thaler et al. 2011). The same study also found that there was no differential activity in auditory cortex. This echolocation related activity in the CC was absent in sighted control participants who were unable to echolocate. In addition, the activity in the CC was stronger in the early blind echolocation expert as compared to the late blind echolocation expert. Importantly, the early blind participant also showed superior echolocation ability compared to the late blind participant. Activation in CC has been linked to visual imagery, i.e. images represented in 'the mind's eye' for sighted people (for reviews see for example Kosslyn et al. 2001; Kosslyn and Thompson 2003), and similar arguments have been made for CC activity in blind people (e.g. Büchel et al. 1998; Lambert et al. 2004). A study by Cui et al. (2007) found a significant positive correlation between sighted people's level of activation in the CC during visual imagery and their scores on a questionnaire that measures the vividness of their visual imagery (vividness of visual imagery questionnaire, VVIQ, Marks, 1973). In sum, higher relative activity in the CC has been linked to both echolocation performance and vividness of visual imagery. Consequently, here we tested if individual differences in vividness of visual imagery (VVI) are related to individual differences in echolocation ability in sighted novices.

To this end our study first sought to replicate the finding of Teng and Whitney (2011) that sighted novices are able to use echolocation to make size discrimination judgments. We then investigated if individual differences in echolocation ability, as measured with Teng and Whitney's (2011) paradigm, are related to individual differences in VVI as measured with Marks' (1973) VVIQ. Furthermore, to investigate the potential role played by participants' hearing abilities, we measured participant's performance in a battery of auditory tests that have shown to correlate with echolocation performance in blind people (Schenkman and Nilsson 2010) and in sighted people who have been trained to echolocate (Carlson-Smith and Wiener 1996).

2. Materials & Methods

All testing procedures were approved by the ethics board at Durham University, and participants gave written informed consent prior to testing. All experimental procedures conformed with the Code of Ethics of the World Medical Association as stated in the Declaration of Helsinki.

2.1. Participants

Participants were recruited from a participation pool of undergraduate students at Durham University. Participants were compensated with course credits or £ 8/hour. 24 participants (7 males) aged between 18 and 38 ($M=22.25$, $SD=3.7$) took part in the study. Two of the participants did not appear for the auditory test battery. All participants reported to have normal hearing and no history of any hearing difficulties. All participants had normal or corrected to normal vision. All participants reported to not have prior experience with echolocation.

2.2. Set-Up and Apparatus

The experiment took place inside a tent-like gazebo structure (300 cm (W) x 300 cm (L) x 280 cm (H)) placed inside a quiet laboratory room. The ceiling of the gazebo was covered with a plastic sheet.

The sides of the gazebo were covered with cotton and fleece blankets on the inside, and surrounded by poster-board walls on the outside.

2.2.1. Echolocation

Participants were seated in the centre of the gazebo on a height adjustable chair. To measure participants' echolocation ability we used the apparatus illustrated in Figure 1, which was placed 33 cm in front of the participant. This apparatus is a replication of the apparatus used by Teng and Whitney (2011). The apparatus consisted of a frame made of metal rods (0.5 cm circular diameter). The frame stood up vertically and had two horizontal crossbars which were spaced 27.5 cm apart. The crossbars were used to mount flat, circular discs made from 0.5 cm thick acrylic. The discs were mounted with a small hook on their back. The front of the discs was painted with primer. The back was covered with felt (to minimize sounds that might have arisen from coming into contact with the crossbars). The largest disc (the reference disc) was 25.4 cm in diameter. The five comparison discs had diameters of 5.1 cm, 9 cm, 13.5 cm, 17.5 cm and 22.9 cm. The angular size differences between the reference and the comparison discs were approximately 31.6, 26.4, 19.8, 13.5 and 4.3 degrees.

<Figure 1>

Figure 1 – Illustration of Apparatus used during the Echolocation Task.

2.2.2. VVIQ

Participants were given the vividness of visual imagery questionnaire (VVIQ) developed by Marks' (1973), which had also been used by Cui et al. (2007). During the VVIQ participants are asked to indicate the vividness of their imagery in response to 16 different questions on a 5-point rating scale, once with their eyes open and once with their eyes closed. Examples of VVI questions are given in the supplementary material. VVIQ instructions and rating scale were presented visually. VVIQ questions were presented aurally. To maximize consistency across participants and sessions a standardized recording of the VVIQ questions had been made and this standardized recording was presented to participants using a laptop computer and headphones.

2.2.3. Auditory Tests

Auditory testing was conducted using an IBM Lenovo N500 laptop (Intel Pentium Dual PCU T3400 2.16 GHz, 3 GB RAM, 64 bit Windows 7 Enterprise SP1). Software used to conduct testing was programmed using Psychophysics Toolbox 3.08 (Brainard 1997) and Matlab (R2009a, The Mathworks, Natick, MA, USA). Sounds were presented using a Creative Sound Blaster X-Fi HD Sound Card (Creative Technology Ltd., Creative Labs Ireland, Dublin, Ireland) and AKG K271 MKII Circumaural Studio Headphones (Harman International Industries, Stamford, CT, USA). The tests in our auditory test battery were selected based on previous research (Carlson-Smith and Wiener 1996; Schenkman and Nilsson 2010). We conducted pure tone hearing threshold measurements for the right and left ears separately, Detection of Change in Intensity (DCI) tests, and Detection of Frequency Modulation (DFM) tests. Please note that our equipment was unsuitable to measure hearing thresholds in absolute units as we did not have access to an audiometer. In the context of the tests and analyses we replicated from previous research, however, this was not a problem because all analyses were conducted relative to individual hearing thresholds. Thus, we first determined individual participant's hearing thresholds

within our set-up, and then used these data for subsequent analyses and to choose parameters for subsequent DCI and DFM tests.

2.3. Task & Procedure

The experiment took place in three sessions that took part on separate days. In both session one and two participants completed the VVIQ first, and the echolocation task second, i.e. each participant completed both the echolocation task and the VVIQ twice (both the eyes open and eyes closed conditions). Each of these sessions took approx. 1 hour and 45 minutes to complete. In session three participants completed the auditory test battery. This session took approx. 1 hour and 15 minutes to complete.

2.3.1. Echolocation

Participants performed the echolocation task in line with the procedure of Teng and Whitney (2011). Participants were asked to close their eyes and to wear a blindfold. They were seated facing the frame at a distance of 33 cm, measured from the front of the frame to the tragus of the participant's ear. The chair was adjusted so that the level of the participant's ear was half-way between the two crossbars. Participants were then asked to practice making tongue-clicks. After the experimenter was satisfied that the participant could produce adequate clicks the participant completed two practice trials, which were followed by 100 test trials. Each trial followed the same pattern: participants were asked to occlude their left and right ear canals with their right and left index finger tips, respectively, whilst the experimenter placed the reference disc (i.e. the bigger disc) on either the top or bottom crossbar and one of the five comparison discs on the remaining crossbar. Once the discs were placed the experimenter stepped behind the participant and signalled with a shoulder tap to unblock their ears. The participant then reported whether they believed the reference disc (i.e. the bigger disc) to be on the top or bottom crossbar (no-click judgment). The purpose of obtaining the no-click judgment was to obtain a level of baseline performance that might take into account any information about disc placement that might be contained in ambient noise or noise that arose during the placing of the discs. The experimenter recorded the no-click judgment. Subsequently, participants began making mouth-clicks. Participants were given up to 10 seconds of clicking to determine whether they believed the reference disc (i.e. the bigger disc) was on the top or bottom crossbar (click judgment). The experimenter recorded the click judgment, before proceeding to the next trial. In line with Teng and Whitney (2011) no feedback was given about the accuracy of participants' judgments. In each session each participant completed a total of 100 trials, 20 for each comparison disc. The placement of discs was randomized so that each comparison disc appeared equally often on top and bottom bars.

2.3.2. VVIQ

As per VVIQ instructions, participants completed the VVIQ once with their eyes open, and subsequently with their eyes closed. In 'eyes closed' conditions participants were asked to close their eyes and to wear a blindfold. In 'eyes open' conditions, participants looked steadily in front of them. They were seated at an empty desk, facing the backside of an opened laptop, with the experimenter sitting behind the laptop. Behind the experimenter was a white wall. VVIQ instructions and rating scale were presented visually in the beginning of each session. Subsequent VVIQ questions were presented aurally, both in eyes closed and in eyes open conditions. This was done so that participants did not have to open their eyes and remove their blindfold in between questions when completing the questionnaire in 'eyes closed' conditions. To maximize consistency across participants, conditions and sessions, a standardized recording of the VVIQ questions was presented

to participants using a laptop computer and headphones. The experimenter recorded the participant's rating given for each question.

2.3.3. Auditory Tests

2.2.3.1. Hearing Thresholds

Hearing thresholds were measured at frequencies of 500, 1000, 2000, 4000 and 6000 Hz. Hearing thresholds were measured separately for the right and left ear using the modified Hughson-Westlake Procedure (e.g. Roeser and Clark 2007). The method uses ascending and descending methods of limits with a single stimulus for measuring the auditory thresholds. The threshold for each ear, frequency and participant was defined as the lowest level at which a listener detected two out of three signal presentations. Each tone was presented for the duration of 2 seconds (incl. 80 ms linear on and off ramp). The onset of each tone was randomized to avoid telegraphing the stimulus to the participant.

2.2.3.2. DCI test

This test was a replication of the test used by Carlson-Smith and Wiener (1996). It measures participant's ability to detect a change in the intensity of a tone. On each trial participants were presented with a continuous tone of 2 second duration (incl. 80 ms linear on and off ramp) at a constant intensity level over which 300 ms intensity increments (jumps in loudness) could be superimposed. To avoid subjects predicting when a jump in loudness occurred, the onset times of the jumps were randomized, with the limitation that the intensity increments began after an 800 ms lead in of the continuous tone. Following Carlson-Smith and Wiener (1996) twelve intensity increments were presented for each increment size of 1.0, 0.8, 0.6, 0.4, 0.2 decibels (dB) at frequencies 500 and 2000 Hz. There were also 24 catch trials for each frequency. Participants were instructed to press a button whenever they detected a jump in loudness. Participants were informed that there were catch trials. Test trials were preceded by a practice series with increments in intensity that gradually decreased from 5 dB to 2 dB. Following Carlson-Smith and Wiener (1996) the DCI was presented at 500 and 2000 Hz at 45 and 35 dB Hearing Threshold (HT), respectively (as determined for our set-up; a single HT value was obtained for each participant by averaging HT across the right and left ears). Carlson-Smith and Wiener (1996) has also conducted a test at 2000 Hz at 30 dB HT. We omitted this test because Carlson-Smith and Wiener (1996) did not find any differences between tests conducted at 35 and 30 dB, and because it reduced testing time for our participants.

2.2.3.2. DFM test

This test was a replication of the test used by Carlson-Smith and Wiener (1996). It measures participants' ability to detect a change in the frequency of a tone. On each trial participants were presented with a pair of tones and they pressed a button whenever they detected a change in the pitch (frequency modulation) in the second tone of a pair. Each pair consisted of a 2-second (incl. 80 ms linear on and off ramp) steady pure tone, followed either by another 2-second (incl. 80 ms linear on and off ramp) that could either be also a steady pure tone, or a frequency modulated tone. There was a 300 ms silent gap in between the two tones. The frequency modulation was 300 ms long. To avoid participants predicting when a frequency modulation would occur, the onset time of the modulations was randomized, with the limitation that modulations could only occur after an 800 ms lead-in of the continuous tone. Participants were informed that the first tone was always a steady tone, and they were told that they could use this as a reference for assessing any changes in the second tone. Participants were also told that there were catch trials. Following Carlson-Smith and Wiener (1996) we used five increments of frequency modulation (1.0, 0.8, 0.6, 0.4, 0.2 percent

modulation) and 12 tests were presented for each increment. There were also 24 catch trials. Tests were conducted at centre frequencies of 500 and 2000 Hz. Test trials were preceded by a practice series with increments in frequency modulation that gradually decreased from 5 to 2 percent. Following Carlson-Smith and Wiener (1996) the DFM was presented at 500 Hz and 2000 Hz at 30 dB HT (as determined for our set-up; a single HT value was obtained for each participant by averaging HT across the right and left ears). Carlson-Smith and Wiener (1996) had also conducted a test at 500 Hz at 45 dB HT. We omitted this test because Carlson-Smith and Wiener (1996) did not find any differences between tests conducted at 30 and 45 dB, and because it reduced testing time for our participants.

2.4. Data Analysis

2.4.1. Echolocation

Percentage correct judgments was calculated separately for each condition (no-click and click), angular size difference between reference and comparison disc (31.6, 26.4, 19.8, 13.5 and 4.3 degrees), and session (one and two). Chance performance was 50%.

2.4.2. VVIQ

We computed participants' average response rating across questions. To compare the test-retest reliability in our sample to values reported by Marks (1973) we averaged scores across eyes open and eyes closed conditions, and correlated scores between sessions one and two. Retinal visual input can lead to differences in the strength of visual imagery (e.g. Keogh and Pearson 2011; Sherwood and Pearson 2010). Thus, for further analysis we analysed 'eyes open' and 'eyes closed' scores separately, but averaged across session one and two. In the VVIQ lower scores denote higher vividness. To make subsequent analyses more intuitive we multiplied scores by -1 so that larger VVI scores denoted more vivid visual imagery.

2.4.3. Auditory Test Battery

Participants' differences in hearing threshold between the right and left ear were computed as the sum of the absolute differences in hearing thresholds (in dB) between the right and left ears across frequencies. Participants' DCI and DFM scores (at 500 and 2000 Hz separately) were computed as the percentage of correct detections minus the percentage of false alarms.

3. Results

3.1. Echolocation

Following Teng and Whitney's (2011) analysis we computed a three-way repeated measures ANOVA with within subject factors of 'session' (one or two), 'clicking' (click or no-click) and 'size', i.e. the angular size difference between reference and comparison disc (31.6, 26.4, 19.8, 13.5 and 4.3 degrees). Mauchly's test was not significant for any of the comparisons, so that sphericity could be assumed. The analysis revealed a significant main effect of clicking ($F(1,23)=17.178$, $p<.000$; $\eta_p^2 = .428$), and inspection of means showed that participants did better when they made clicks (mean = 62.3; SD = 12.04) as compared to when they remained silent (mean = 50.9; SD = 3.2). The click x size interaction was significant as well ($F(4,92)=5.454$, $p=.001$; $\eta_p^2 = .192$), and so was the click x session interaction ($F(1,23)=7.097$, $p=.014$; $\eta_p^2 = .236$). No other effects were significant. Figure 2A shows accuracy scores averaged across participants, separately for sessions one and two, click and no-click conditions, and the five size differences. Figure 2B shows accuracy scores averaged across sessions

one and two. Figure 2C shows accuracy scores averaged across participants and disc sizes. It is evident from the significant clicking x size interaction effect and Figure 2B that the benefit of clicking depended on the angular size differences between the reference and comparison disc, i.e. clicking is more beneficial for angular size differences larger than 4.3 degrees. It is evident from the significant clicking x session interaction effect and Figure 2C that participants improved from session one to two, but only for the clicking condition, whereas their ‘guessing’ rate remained stable.

<Figure 2>

Figure 2 – Participants’ performance in the echolocation task. **(A)** Accuracy scores averaged across participants, separately for sessions one and two, click and no-click conditions, and the five size differences. **(B)** Accuracy scores are shown averaged across participants and sessions one and two. **(C)** Accuracy scores are shown averaged across participants, and disc sizes. In all plots, error bars denote SEM across participants. Results of post-hoc paired t-tests (Bonferroni corrected) for data shown in **B** and **C** are indicated with asterisks (* $p < .05$, ** $p < .01$, *** $p < .001$).

To support the interpretation that participants used clicking to successfully echolocate, we used one-sample t-tests to determine if click and no-click scores, averaged across disc sizes, differed from chance (50%). The analysis revealed that click scores differed significantly from chance (session 1: $t(23)=3.643$, $p=.001$; session 2: $t(23)=5.171$; $p<.001$), whereas no-click scores did not differ significantly from chance (session 1: $t(23)=1.395$, $p=.176$; session 2: $t(23)=.648$; $p=.524$). Thus, participants used clicking to successfully echolocate, as opposed to simply guessing in the no-click condition.

3.2. VVIQ

Participants average VVIQ scores (mean = -2.31; SD = 0.32) did not differ significantly from those reported by Cui et al. (2007) (scores estimated from Figure 1C in Cui et al (2007): mean = 2.3; SD = 0.6; Note: Cui et al. (2007) did not multiply by -1, but we did for the purpose of comparison) (independent samples t-test: $t(30)=0.0608$; $p=0.9520$). VVIQ scores were significantly higher in ‘eyes closed’ (mean = -2.03; SD = 0.42) than in ‘eyes open’ conditions (mean=-2.58; SD = 0.29) ($t(23)=7.9018$; $p<.001$). VVIQ test-retest reliability computed for our sample was 0.7, which is similar to the value of 0.74 (N=68) reported by Marks (1973).

3.3. Auditory test battery

Summary statistics for participants’ performance in the battery of hearing tests we conducted are shown in Table 1. Values for DCI and DFM at 2000 Hz and difference thresholds between right and left ears (for sighted participants) were not reported in previous reports. Carlson-Smith and Wiener (1996), however, did report scores for DFM and DCI tests at 500 Hz (though please note that they excluded DFM performance at 1% from statistical analysis). Performance of our sample does not differ from performance of the sample in Carlson-Smith and Wiener’s (1996) study for DFM 500 Hz (scores estimated from Figure 1 in Carlson-Smith and Wiener (1996): DFM 500 Hz: mean= 39; SD= 3) (independent samples t-test; $t(29) =1.3572$; $p =0.1852$), or DCI at 500 Hz (scores estimated from Figure 1 in Carlson-Smith and Wiener (1996): DCI 500 Hz: mean=27; SD=12) (independent samples t-test; $t(29) =2.0214$; $p=0.0526$).

<Table 1>

Table 1 – Means and SD (in parenthesis) of participants' performance in the battery of hearing tests. Absolute hearing threshold difference scores (Abs HT Diff) are given in dB. For the other tests performance was computed as the percentage of correct detections minus the percentage of false alarms.

3.4. Relationship between Echolocation and VVIQ

To investigate the relationship between echolocation ability and VVI we computed a correlation analysis. Echolocation Ability scores were calculated as the difference in performance between click and no-click conditions averaged across sessions one and two. VVI scores were split into 'eyes open' and 'eyes closed' conditions. VVIQ data are ordinal rather than scale due to being acquired from a rating scale. Thus, we computed both parametric Pearson correlations (r) and non-parametric Spearman's rho (r_s). Both parametric and non-parametric correlations between VVI Eyes Closed and Echolocation Ability were positive and highly significant ($r(24) = .56$; $p = .004$; $r_s(24) = .627$; $p = .001$). Thus, people that have more vivid visual imagery whilst their eyes are closed also have better echolocation ability (or vice versa). This relationship between VVI Eyes Closed and Echolocation Ability is illustrated in Figure 3A. Correlations between VVI Eyes Open scores and Echolocation Ability were not significant ($r(24) = .266$; $p = .209$; $r_s(24) = .309$; $p = .142$). This lack of relationship between VVI Eyes Open scores and Echolocation Ability is illustrated in Figure 3B.

<Figure 3>

Figure 3 – (A) Participants' Vividness Score (Eyes Closed) plotted against their echolocation ability. (B) Participants' Vividness Score (Eyes Open) plotted against their echolocation ability. Echolocation ability was calculated as the difference in performance between click and no-click conditions, averaged across disc sizes and session one and two. Larger vividness scores indicate more vivid imagery. Pearson correlations (r) and non-parametric Spearman's rho (r_s) are indicated in each plot. Lines are best fitting linear regression lines.

3.5. Influence of Hearing Ability

To consider the potential influence of the participants' auditory abilities together with their VVI scores, we conducted a multiple linear regression analysis. Specifically, we predicted participants' echolocation ability based on their VVI scores and their performance in our hearing tests. In a first analysis we included all five hearing measures in addition to the VVI (Eyes Closed) scores. This analysis showed that only predictor VVI (eyes closed) (standardized beta = .631, $t_{(15)} = 4.023$, $p = .001$) contributed significantly to the overall model ($F_{(6,15)} = 6.454$, $p = .002$, $R^2 = .721$), whereas none of the other predictors contributed significantly to the regression model. Subsequently we used stepwise linear regression to determine significant contributions of any of the hearing variables in particular. The stepwise regression showed that predictors VVI (eyes closed) (standardized beta = .452, $t_{(19)} = 2.995$, $p = .007$) and DCI at 500 Hz (standardized beta = .526, $t_{(19)} = 3.481$, $p = .002$) contributed significantly to the overall model ($F_{(2,19)} = 13.629$, $p = <.001$, $R^2 = .589$), whereas none of the other predictors were significant. We followed the regression result up by computing non-parametric correlation coefficients (Spearman's Rho) between each of the hearing variables and echolocation ability. Consistent with the regression result, the results of this analysis was significant for DCI at 500 Hz ($r_s(22) = .556$; $p = .007$), but the p-value was not even close to significance for any of the other variables. Inspection of the residuals from the stepwise regression showed that residuals were normally distributed (Shapiro-Wilk $W(22) = .917$; $p = .066$) and that there was no evidence of

heteroscedasticity. In sum, the data suggest that participants' ability to discriminate intensity modulations at 500 Hz is related to their echolocation ability.

4. Discussion

Consistent with previous results (Teng and Whitney 2011) we showed that sighted echo-naïve participants successfully used click-based echolocation to make size discrimination judgements. In addition, we found that there was a positive relationship between the vividness of a sighted novice's visual imagery generated with their eyes closed (i.e. eyes closed and wearing a blindfold) and their ability to make accurate size discrimination judgments using echolocation. This relationship remained significant even when differences in hearing ability were statistically controlled for. Although we found an association between echolocation ability and VVI with eyes closed, there was no association between echolocation ability and VVI with eyes open. Retinal visual input can interfere with visual imagery (e.g. Keogh and Pearson 2011; Sherwood and Pearson 2010), and consistent with this, VVI scores in our study were lower with eyes open. As such, VVI scores obtained whilst participants had their eyes closed can be considered a more 'pure' measure of visual imagery, and therefore it is perhaps not surprising that we found a significant relationship. In sum, our study provides novel evidence that individual differences in echolocation ability are associated with individual differences in vividness of visual imagery (VVI). Before we discuss the implications of these data further we will address how our data fit with previous reports.

4.1. Relationship to previous echolocation size-discrimination data – Teng and Whitney (2011)

Consistent with previous results (Teng and Whitney 2011) we showed that sighted echo-naïve participants successfully used click-based echolocation to make size discrimination judgements. We replicated the results by Teng and Whitney (2011) that participants' echolocation skills improve with practice. We also show that performance is better for larger size discrepancies between target and reference disc, which appears to agree with results by Teng and Whitney (2011) (compare their Fig.3). Those authors, however, did not report post-hoc test results between click and no-click conditions for the various disc sizes, so that a direct comparison is not possible. Average performance in click conditions in our study was 62.3%. In contrast, average performance in Teng and Whitney's (2011) study was around 70% (estimated from their Fig.3A). Similarly, average best performance in a single condition in our study was 69% (compare Fig.2A), whereas it was about 80% in Teng and Whitney's (2011) study (estimated from their Fig.3A). Thus, there appears to be a roughly 10% discrepancy both in terms of average and in terms of maximum performance. We do not know what the cause of this difference is, but we think that differences in room acoustics are the most likely explanation, since neither study was conducted in a soundproof and/or anechoic room.

4.2. Relationship to previous investigations of hearing ability for echolocation - Carlson-Smith and Wiener (1996)

Variations in sound frequency (pitch) and intensity (loudness) are likely auditory cues used during echolocation (Cotzin and Dallenbach 1950; Papadopoulos et al 2011; Rosenblum et al 1995; Schenkman and Nilsson 2010; 2011; Stoffregen and Pittenger 1995). In agreement with this expectation Carlson-Smith and Wiener (1996) found that the ability to discriminate sound intensity (DCI) and frequency (DFM) was related to better echolocation performance in their study. In their study, however, they only found a relationship between echolocation ability and performance on DCI and DFM at 500 Hz, but not for performance on DCI or DFM test at 2000 Hz. The authors argued that the lack of relationship with respect to 2000 Hz might have been due to the echolocation task employed, which required participants to listen to acoustic reverberations arising from their own

foot-steps while walking, which might have resulted in informative reverberations in lower, but not higher frequency bands. In agreement with this idea Ashmead et al (1998) provided a model and measurements of ambient sound fields suggesting that variations in frequency bands of 500 Hz or below are informative during a locomotion task that requires participants to listen to acoustic reverberations arising from their own foot-steps while walking. Importantly, in our current task, participants made mouth clicks which have considerable energy in higher frequency bands (Rojas et al. 2009; Thaler et al. 2011). Yet, we replicated Carlson-Smith and Wiener's (1996) results with regard to the positive relationship between performance on the DCI test at 500 Hz and echolocation, and the lack of a statistical relationship between performance on DCI and DFM test for 2000 Hz. In contrast to Carlson-Smith and Wiener (1996), we did not find a relationship between DFM at 500 Hz and echolocation ability, however. There is the possibility that differences in results between our study and Carlson-Smith and Wiener (1996) might be due to the sample, i.e. we worked with a sample of sighted echo-naïve participants whereas those authors worked with a sample of sighted echo-trained participants. There is also the possibility that this is due to a difference in echolocation tasks. Broadly, however, our data agree with Carlson-Smith and Wiener (1996) and suggest that the ability to discriminate changes in intensity of a 500 Hz sound might be relevant for echolocation. Without any recordings of the echo stimuli used, however, the connection between this auditory measure and our echolocation task remains a matter of speculation.

4.3. Underlying Mechanisms for Correlation between Echolocation and Imagery

With regard to the underlying mechanisms, we suggest two explanations. One potential explanation is that the association between echolocation ability and VVI is due to the fact that sighted novices use visual imagery to make echolocation judgements. For example, the spatial information provided by echoes might be turned into a visual image of the environment from which an echolocator picks out the relevant information needed to make an accurate judgment. Those with lower VVI produce lower resolution images, providing less detail, explaining why they can make less accurate judgments. Those with higher VVI are able to produce higher resolution images enabling them to make more accurate judgements. This interpretation assumes that visual imagery is pictorial rather than symbolic (see Kosslyn and Thompson 2003, for a review of theories of visual imagery). Participants in our study did not report having a conscious experience of a visual representation of the environment whilst performing the echolocation task. Yet, this does not rule out this explanation.

Importantly, however, correlation between two variables does not signify a causal relationship. Thus, an alternative (though not mutually exclusive) explanation is that both visual imagery and echolocation rely on a third, shared ability, and that differences in this ability determine both VVI and echolocation scores. There is the possibility that the ability shared across VVI and echolocation is the ability to recruit calcarine cortex for tasks that do not rely on retinal input. Both visual imagery and echolocation involve processing of information retrieved from sources external to the visual system (memory, or auditory systems, respectively), yet both VVI and echolocation have been linked to activity (as measured with fMRI) in calcarine cortex. It has been suggested previously that calcarine cortex, i.e. early 'visual cortex, has supra-modal capabilities which contribute to performance on non-visual tasks in the sighted as well as in the blind (e.g. Pascual-Leone and Hamilton 2001). Thus, the ability shared across VVI and echolocation might be the ability to recruit calcarine cortex for tasks that do not rely on retinal input. In this way, sighted people who have better ability to recruit CC for non-visual input would score higher in both VVI and echolocation, hence causing a positive correlation between VVI and echolocation ability.

Support for this explanation comes from the literature about neuroplasticity in response to vision loss. Specifically, as laid out in the introduction, blind people typically show better echolocation

performance than sighted people (see Teng and Whitney 2011, for a summary). Furthermore, blind people also show increased activation in calcarine cortex for non-visual stimuli, such as touch and sound (for reviews see Bavelier and Neville 2002; Merabet and Pascual-Leone 2010), and TMS studies show that CC in the blind brain is functionally relevant for performance in non-visual tasks (Cohen et al. 1997) . In addition, within a group of blind people a positive correlation has been observed between age at onset of vision loss and echolocation ability such that people who lost sight earlier in life are better at echolocation (Teng et al. 2012). Most interestingly, positive correlations have also been observed between age at onset of vision loss and strength of CC activations in response to non-visual stimuli, so that people who have lost vision earlier in life tend to have stronger CC activations (Cohen et al. 1999; Sadato et al. 2002). In summary, both echolocation ability and activation in CC in response to non-visual input are increased in blind as compared to sighted people, and within groups of blind people both correlate positively with age at onset of vision loss. This is consistent with the idea that the positive relationship between VVI and echolocation that we observe in our sighted sample might be due to people’s underlying differences in their ability to recruit calcarine cortex for tasks requiring non-visual input.

4.4. Generalization of Findings to other echolocation tasks

One constraint on interpretation is that we tested only a single aspect of echolocation ability: perception of relative size. As laid out in the introduction, however, humans have demonstrated remarkable echolocation sensitivity to a variety of other aspects of the environment, such as density, distance, location and motion. We argue above that the correlation between VVI and echolocation ability in our study may be grounded in the recruitment of calcarine cortex for both VVI and the echolocation task. Thus, we would expect this relationship between VVI and echo ability to generalize to other echolocation tasks, unless performance in the echolocation task did not involve calcarine cortex. In recent work we have shown that processing of echo-motion in blind and sighted people relies on activity in temporal-occipital, rather than calcarine cortex (Thaler et al. 2013a). Based on this we would expect that performance in an echolocation task that relies exclusively on processing of echo-motion should not correlate with VVI. Future research is needed to test this.

4.5. Generalization of Findings to Blind People

Our study investigated the relationship between visual imagery and echolocation in sighted people. Future research should address this relationship in the blind. Importantly, even though tests of visual imagery might be adapted for people with residual vision or for people who are totally blind but have had visual experience earlier in life, an adaptation is more challenging for people who are totally blind from birth (Cattaneo et al. 2008; Kaski 2002; Kerr 1983; Zimler and Keenan 1983). For example, one could argue that the concept of ‘visual’ imagery may not be applicable to someone who never had any visual experience. That said, there are aspects of vision that could be considered not visual per se, but ‘supra-modal’ and that could therefore also be obtained from other modalities. An example for a ‘supra-modal’ aspect of vision is the sense of spatial layout of an environment that can not only be gained from vision, but also from audition or touch. An example for a non-supra modal aspect of vision is colour. Stoffregen and Pittenger (1995) touched upon the issue of supra-modality when they proposed that perceptual systems are sensitive to higher order relationships among sensory events. The important point is that these higher order relationships can only arise for events that can be processed across modalities, i.e. events that we consider supra-modal. In sum, the concept of ‘visual’ imagery might still apply to a congenitally blind person, but in the case of imagery involving spatial layout, for example, it might be more appropriately termed ‘spatial’ imagery. Furthermore, previous investigations of visual imagery in people with varying degrees of blindness suggest that the effects of blindness on imagery may depend not only on visual experience before blindness, but also on the nature of blindness, e.g. whether partial vision is present and

whether it is central or peripheral vision that is lost (Dulin et al. 2008). In sum, various factors have to be carefully considered in the investigation of imagery in the blind. This would however not prevent the investigation of imagery in the blind and its relationship to echolocation.

4.6. Implications for Training

Our current findings may have implications for echolocation training, in particular for people who are sighted but likely to lose vision due to surgery or disease. For example, echolocation training augmented with VVI practice may be favourable to echolocation training alone. Although Rademaker and Pearson (2012) recently reported that imagery strength did not improve when participants practised for an hour over five consecutive days, longer training durations may show an effect. Furthermore, assessments of VVI may provide indications of the extent to which echolocation ability might be attainable.

Acknowledgments

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Figure Captions

Figure 1 – Illustration of Apparatus used during the Echolocation Task.

Figure 2 – Participants’ performance in the echolocation task. **(A)** Accuracy scores averaged across participants, separately for sessions one and two, click and no-click conditions, and the five size differences. **(B)** Accuracy scores are shown averaged across participants and sessions one and two. **(C)** Accuracy scores are shown averaged across participants, and disc sizes. In all plots, error bars denote SEM across participants. Results of post-hoc paired t-tests (Bonferroni corrected) for data shown in **B** and **C** are indicated with asterisks (* $p < .05$, ** $p < .01$, *** $p < .001$).

Figure 3 – **(A)** Participants’ Vividness Score (Eyes Closed) plotted against their echolocation ability. **(B)** Participants’ Vividness Score (Eyes Open) plotted against their echolocation ability. Echolocation ability was calculated as the difference in performance between click and no-click conditions, averaged across disc sizes and session one and two. Larger vividness scores indicate more vivid imagery. Pearson correlations (r) and non-parametric Spearman’s rho (r_s) are indicated in each plot. Lines are best fitting linear regression lines.

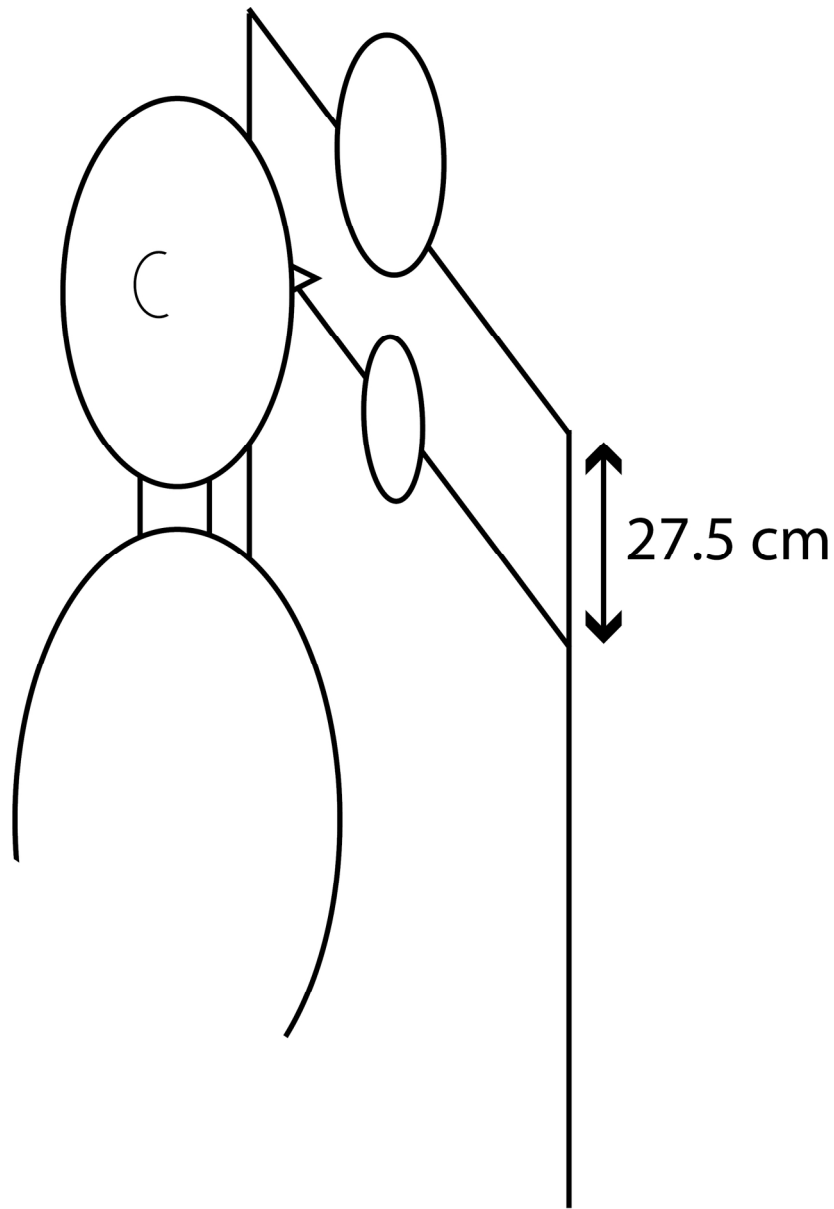


Figure 1 – Illustration of Apparatus used during the Echolocation Task.
79x104mm (600 x 600 DPI)

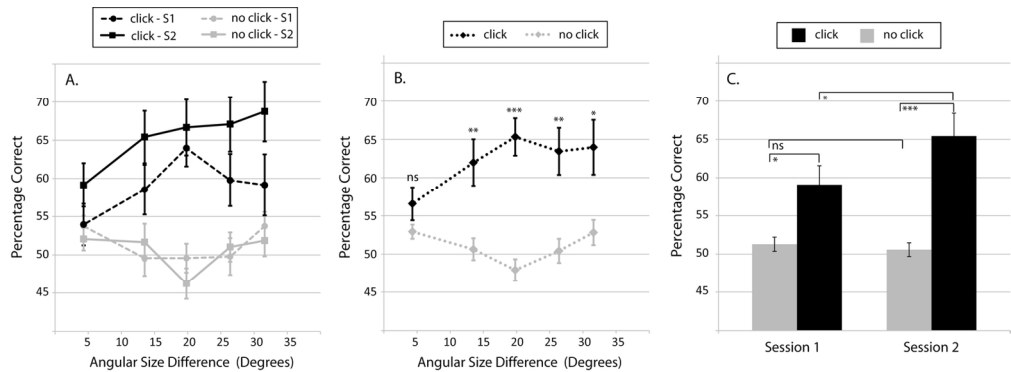


Figure 2 – Participants' performance in the echolocation task. (A) Accuracy scores averaged across participants, separately for sessions one and two, click and no-click conditions, and the five size differences. (B) Accuracy scores are shown averaged across participants and sessions one and two. (C) Accuracy scores are shown averaged across participants, and disc sizes. In all plots, error bars denote SEM across participants. Results of post-hoc paired t-tests (Bonferroni corrected) for data shown in B and C are indicated with asterisks (*p<.05, **p<.01, *** p<.001).

141x51mm (300 x 300 DPI)

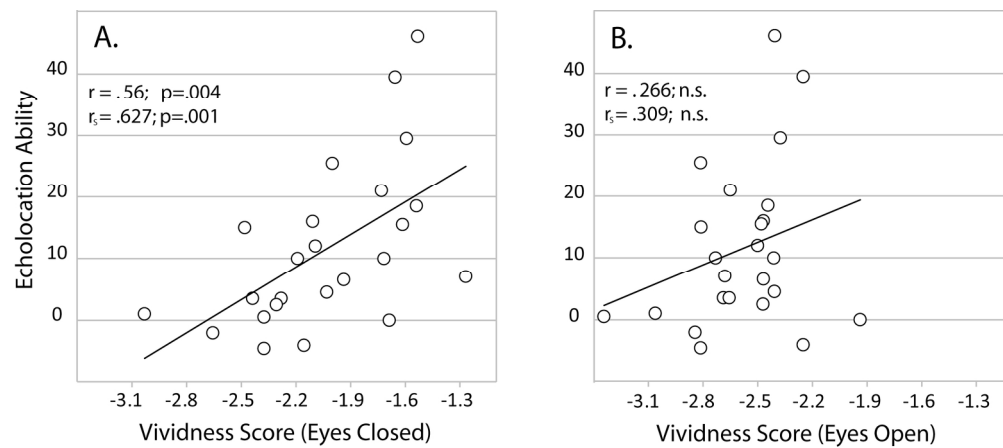


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Table 1 – Means and SD (in parenthesis) of participants’ performance in the battery of hearing tests. Absolute hearing threshold difference scores (Abs HT Diff) are given in dB. For the other tests performance was computed as the percentage of correct detections minus the percentage of false alarms.

Abs HT Diff	DCI 500 Hz	DCI 2000 Hz	DFM 500 Hz	DFM 2000 Hz
18 (7) dB	15 (16) %	12 (14) %	50 (24) %	58 (21) %

Supporting Material

Correlation between Vividness of Visual Imagery and Echolocation Ability in Sighted, Echo-Naïve People
Lore Thaler, Rosanna C. Wilson, Bethany K. Gee

VIVIDNESS OF VISUAL IMAGERY QUESTIONNAIRE (VVIQ) --- Adapted from Marks DF (1973) Visual imagery differences in the recall of pictures. *British J Psychol* 1: 17-24

The Rating Scale Used in the VVIQ

Rating	Description
1	Perfectly clear and as vivid as normal vision
2	Clear and reasonably vivid
3	Moderately clear and vivid
4	Vague and dim
5	No image at all, you only "know" that you are thinking of an object

Items contained in the VVIQ

In answering items 1 to 4, think of some relative or friend whom you frequently see (but who is not with you at present) and consider carefully the picture that comes before your mind's eye.

Item	
1	The exact contour of face, head, shoulders and body.
2	Characteristic poses of head, attitudes of body etc.
3	The precise carriage, length of step, etc. in walking.
4	The different colours worn in some familiar clothes.

Visualize the rising sun. Consider carefully the picture that comes before your mind's eye.

Item	
5	The sun is rising above the horizon into a hazy sky.
6	The sky clears and surrounds the sun with blueness.
7	Clouds. A storm blows up, with flashes of lightening.
8	A rainbow appears.

Think of the front of a shop which you often go to. Consider the picture that comes before your mind's eye.

Item	
9	The overall appearance of the shop from the opposite side of the road.
10	A window display including colours, shape and details of individual items for sale.
11	You are near the entrance. The colour, shape and details of the door.
12	You enter the shop and go to the counter. The counter assistant serves you. Money changes hands.

Finally, think of a country scene which involves trees, mountains and a lake. Consider the picture that comes before your mind's eye.

Item	
13	The contours of the landscape.
14	The colour and shape of the trees.
15	The colour and shape of the lake.
16	A strong wind blows on the tree and on the lake causing waves.